RADIATION-INDUCED INHERITED STERILITY IN *Heliothis zea* (BODDIE)

By

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TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES	vi
LIST OF FIGURES	viii
ABSTRACT	ix
CHAPTER ONE GENERAL INTRODUCTION	1
CHAPTER TWO REVIEW OF LITERATURE	5
Sterile Insect Technique	5
Hybrid Sterility	8
Inherited Sterility	10
CHAPTER THREE INHERITANCE OF RADIATION-INDUCED DELETERIOUS EFFECTS	18
Materials and Methods	18
Results	20
CHAPTER FOUR FIELD SURVIVAL OF LARVAE FROM IRRADIATED PARENTS	37
Materials and Methods	37
Results	38
CHAPTER FIVE EFFECTS OF IONIZING RADIATION AND INHERITED STERILITY ON MATING COMPETITIVENESS	45
Materials and Methods	45
Results	48
CHAPTER SIX MATING PROPENSITY OF FEMALES WITH DIFFERENT MATING HISTORIES	60
Materials and Methods	60
Results	61

CHAPTER SEVEN
DISCUSSION 67

Effects of Radiation and Inherited Sterility on Reproduction 67
Field Survival of Larvae From Irradiated Parents 68
Effects of Radiation and Inherited Sterility on Mating Competitiveness 69
Mating Propensity of Females with Different Mating Histories 71

CHAPTER EIGHT
GENERAL CONCLUSIONS 72

REFERENCES 74

BIOGRAPHICAL SKETCH 86

LIST OF TABLES

Table		Page
1	Effects of gamma irradiation of male corn earworm adults on reproduction of P_1 adults (P_1 adults irradiated ca. 12 h after emergence)	24
2	Effects of gamma irradiation of female corn earworm adults on reproduction of P_1 adults (P_1 adults irradiated ca. 12 h after emergence)	25
3	Effects of gamma irradiation of corn earworm adults on reproduction of P_1, F_1, and F_2 adults (P_1 adults irradiated with 10 krad ca. 12 h after emergence)	26
4	Effects of gamma irradiation on H. zea reproduction when descendents from irradiated P_1 adults are backcrossed to P_1 adults (adults irradiated with 10 krad ca. 12 after emergence)	28
5	Effects of gamma irradiation on reproduction of P_1 and F_1 adults when H. zea are irradiated as pharate adults (mature pupae) and 12-h-old adults	30
6	Response of H. zea to different doses of radiation when irradiated males (treated ca. 12 h after emergence) are outcrossed to normal females	32
7	Response of H. zea to different doses of radiation when irradiated adults (treated ca. 12 h after emergence) are inbred	33
8	Comparison of field survival between H. zea from normal and irradiated parents when sweet corn was infested with 5 eggs per plant	41
9	Comparison of field survival between H. zea from normal and irradiated parents when sweet corn was infested with 50 eggs per plant	42
10	Comparison of field and laboratory survival between H. zea from normal and irradiated parents	43
11	Estimated rate of increase from P_1 to F_1 generation for H. zea from normal and irradiated parents when reared under laboratory and field conditions	44

Table		Page
12	Mating competitiveness of H. zea moths treated (T) with gamma radiation vs. normal (N) moths in 9 by 30 m screened field cages	51
13	Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared males when released in each of two 0.4-ha areas planted with tobacco	52
14	Comparison of the nocturnal behavior of wild and laboratory-reared (irradiated and normal) H. zea males in each of two 0.4-ha areas planted with tobacco	53
15	Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared females when released in a 2-ha cotton field	54
16	Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared females when released in a 2-ha cotton field	55
17	Nocturnal behavior of normal and irradiated (10 krad, released 30 h after treatment) H. zea laboratory-reared males when released in a 2-ha cotton field	56
18	Comparison of the nocturnal behavior of wild and laboratory-reared (irradiated and normal) H. zea males in a 2-ha cotton field	57
19	Attractiveness of virgin females, females mated to normal males, and females mated to irradiated males in luring H. zea to traps	63
20	Attractiveness of virgin females, females mated to F_1 males (progeny from irradiated (10 krad) male x normal female), and females mated to normal males in luring H. zea males to traps	64
21	Comparison of mating propensity of H. zea females mated once to normal males and held for 24 h, and H. zea females mated once to irradiated (10 krad) males and held for 24 h	65
22	Comparison of mating propensity of H. zea females mated once to normal males and held for 24 h, and H. zea females mated once to F_1 males (progeny from irradiated (10 krad) male x normal female) and held for 24 h	66

LIST OF FIGURES

Figure		Page
1	Female Heliothis zea (Boddie) (Lepidoptera: Noctuidae) adult	34
2	Male Heliothis zea (Boddie) (Lepidoptera: Noctuidae) adult	35
3	Cobalt 60 Gammarad Irradiator (Model GR-12) located at the USDA-ARS Insect Biology and Population Management Research Laboratory, Tifton, Ga.	36
4	Screened field cages (9 x 30 x 4.1 m covered with Saran® screen) used in mating propensity studies ..	58
5	Cone-75-50 trap (Hartstack et al. 1979) baited with Heliothis zea female sex pheromone	59

Abstract of Dissertation Presented to the Graduate School
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Heliothis zea (Boddie) (Lepidoptera: Noctuidae) males and females were irradiated with substerilizing doses of radiation. These moths were inbred and outcrossed and observed for their ability to reproduce. The inherited deleterious effects resulting from the irradiated P_1 males were recorded for several generations. Larvae from both irradiated (10 krad) and normal parents were compared for their ability to survive under field conditions on whorl-stage sweet corn and these results were compared with those from a laboratory study using meridic diet. Irradiated males and females and F_1 males from an irradiated (10 krad) male x normal female cross were released in the field and in field cages and observed for their ability to search/attract and secure a mate. Females that had mated with normal and irradiated (10 krad) males were studied to determine the effect of different mating histories on the subsequent mating propensity of the females.

A 10-krad dose of radiation induced deleterious effects which were inherited through the F_2 generation. These radiation-induced deleterious effects were similar to those reported in other species of Lepidoptera. The relationship between the survival of normal larvae and larvae from irradiated parents was similar under laboratory and field rearing conditions. Irradiated (10 krad) laboratory-reared males and females were competitive with normal laboratory-reared moths in mating, and this competitiveness was not affected by the time interval between irradiation and release, by the mating status of the male, or by the time interval between mating and release. Females mated to normal males and males irradiated with 10 krad had the same mating propensity and experienced the same intermating interval. These effects of substerilizing doses of radiation and inherited sterility on the reproductive ability and behavior of *H. zea* suggest that a great potential exists for population suppression.

CHAPTER ONE
GENERAL INTRODUCTION

Lepidopteran species include some of the most destructive insect pests of agriculture, forests, and stored products. Species of this order severely limit food and fiber production throughout the world. Heliothis zea (Boddie), the corn earworm (CEW), exemplifies the destructive nature of many lepidopteran pests. This insect was recognized as a pest in the United States in 1820, and the larval stage was reported on 72 species of plants (Quaintance and Brues 1905). The preferred host of the CEW is corn (Quaintance and Brues 1905, Isely 1935, Lincoln and Isely 1947, and Hardwick 1965); however, in the United States, the greatest economic damage is sustained when the CEW feeds on cotton. Total economic losses caused by the CEW in the southeastern United States during 1981 were estimated at $134.7 million (Sterling 1983).

The CEW is widely distributed throughout North and South America. It is a seasonal migrant as far north and south as the 52nd parallels of latitude, being recorded from Saskatoon, Saskatchewan, in the north to the Falkland Islands in the south (Hardwick 1965). The areas inhabited by the CEW range in elevation from sea level to more than 3000 m above sea level. The highly diverse climatic conditions to which the CEW has adapted are a manifestation of the great genetic heterozygosity of this insect (Hardwick 1965).

Continuous generations of the CEW are limited to southern Florida and southern Texas in the contiguous United States. The expanded or seasonal range of distribution occurs because of overwintering diapausing pupae and adult dispersal. Felt (1925) and Metcalf and Flint (1939) agreed that diapausing pupae rarely would survive winter conditions north of the 40th parallel. However, Blanchard (1942) reported several records of winter pupal survival in more northerly areas. The contribution of overwintering pupae to subsequent local populations has not been determined. Hardwick (1965) suggested that northward seasonal movements of CEW adults into areas where pupae overwinter are mainly responsible for early seasonal infestations since in many locations the first local infestation of crops evidently occurs before the first emergence of overwintering pupae. This theory has been supported by many studies which have shown that the first capture of CEW adults also occurs before the first emergence of overwintering pupae (Parencia 1964, Stadelbacher and Pfrimmer 1972, Slosser et al. 1975, Hartstack et al. 1982). Other studies have suggested that adult dispersal is very important in annual expansion of CEW into areas in which continuous generations do not occur because of the ability of CEW adults to disperse long distances (Sparks 1972, Haile et al. 1975, and Sparks et al. 1975) and the frequent occurrence of both meteorological conditions and CEW adult behavior conducive to long-range atmospheric transport (Pedgley 1980, Lingren and Wolf 1982, Wolf et al. 1985, Westbrook 1985).

Many control measures have been recommended to reduce the damage caused by the CEW. These measures include manipulation of planting dates, crop rotation, use of resistant varieties, oviposition

repellents, and trap crops, the destruction of the larval stage by mechanical or chemical means, and importation, conservation, and/or mass rearing and release of parasites and predators. The most widely promoted and most successful control measure has been the use of insecticides directed at the larval stage (Hardwick 1965). However, at one time or another the CEW has developed relatively high levels of resistance to all generic types of insecticides available for its control except the pyrethroids (Sparks 1981, Wolfenbarger et al. 1981, Harris et al. 1972). Although H. armiger (Hübner), a close taxonomic relative of the CEW, has developed resistance to pyrethroids in Australia (Gunning and Easton 1984), a panel of U.S. experts chaired by Dr. D. F. Clower, LSU, (Clower et al. in press) found no authentic data for CEW resistance to pyrethroids in the U.S..

Insecticide resistance and the mounting concern over pesticide pollution encouraged scientists to seek new methods of insect control. Three genetic methods have been researched for the control of lepidopteran species: the sterile insect technique, inherited sterility, and hybrid sterility (LaChance 1983). Knipling (1979) listed situations in which these genetic control methods would be most practical and economical. In each of these situations, genetic control methods were applied to pest populations that had not reached high densities or were integrated with other suppressive measures to initially lower the insect density. Each of the three genetic control methods has been studied and/or suggested as a potential control strategy for the CEW (Snow et al. 1971, North and Holt 1970, LaChance 1983).

This research investigated the potential use of inherited sterility as a control strategy for the CEW. Three major areas of study were undertaken: (i) effects of substerilizing doses of radiation and radiation-induced inherited sterility on the reproductive capacity of CEW; (ii) field survival of F_1 larvae from parents irradiated with a substerilizing dose of radiation; and (iii) the effects of a substerilizing dose of radiation and radiation-induced inherited sterility on the mating competitiveness of CEW adults.

CHAPTER TWO
REVIEW OF LITERATURE

Sterile Insect Technique

History and Successful Programs

Genetic techniques for insect control include sterile insect releases, inherited sterility, hybrid sterility, compound chromosomes, conditional lethal factors, cytoplasmic incompatibility, genetic sexing methods, and many others. The sterile insect technique (SIT) is the best known genetic method for the suppression of insect pest populations. While many genetic methods produce a sterile insect, LaChance (1983) defines SIT as the mass rearing of large numbers of insects, complete sterilization of these insects using ionizing radiation or chemosterilants, and the subsequent release of these sterile insects to mate with insects from the native population. Other terms used to describe this genetic method include the sterile release method (SRM), sterile insect method (SIM), and sterile insect release method (SIRM). Any insect species which reproduces sexually is a potential candidate for SIT; however, most major SIT programs have been directed toward dipteran species.

The first widespread use of SIT was the eradication of the primary screwworm, Cochliomyia hominivorax (Coquerel), from North America. The screwworm fly was eradicated from Curacao in 1954 (Baumhover et al. 1955, Knipling 1955), the southeastern United States in 1959 (Baumhover et al. 1959, Knipling 1960), and the southwestern United States in 1964

(LaChance et al. 1967) (considered a foreign pest after 1964). Currently, the screwworm fly has been eradicated from the United States, Baja California, and all of Mexico except the Yucatan peninsula. Other successful SIT programs include the eradication of the Mediterranean fruit fly, Ceratitus capitata (Wied.), from 3 million hectares in Mexico (Patton 1982), and the melon fly, Dacus cucurbitae Coquillett, and the oriental fruit fly, Dacus dorsalis Hendel, from several islands south of Japan (Koyama 1982).

Usefulness on Lepidopteran Species

The successful eradication of the screwworm fly prompted many researchers to investigate the use of SIT for suppressing populations of lepidopteran species. A major problem countered with these studies was that a very high dose of radiation (30-50 kilorads) was required to fully sterilize the lepidopteran species compared to the low doses (< 10 kilorads) needed to sterilize most dipteran species (LaChance 1967, North 1975). These high radiation doses not only sterilized the insects but caused deleterious effects including shortened life span, decreased sexual activity, failure to disperse after release, reduced ability to transfer spermatophores, decreased ability to inseminate females with eupyrene sperm, and asynchrony in biological rhythms (North and Holt 1970, Hutt and White 1974, White et al. 1975, Souka et al. 1975, Van Steenwyck et al. 1979, Sokolowski and Ski 1980, LaChance 1983). However, certain SIT programs involving lepidopteran species have demonstrated a limited amount of success. The codling moth, Laspeyresia pomonella (L.), was controlled in a commercial orchard in the Okanagan Valley in Canada by releasing sterile males over a 3-year period (Proverbs et al. 1969, Proverbs 1970). Also, SIT was used to control

the tobacco hornworm, Manduca sexta (L.) on the island of St. Croix, U. S. Virgin Islands (Snow et al. 1976). Both of these studies were conducted under somewhat isolated conditions and on a relatively small scale. The largest SIT program conducted against lepidopteran species was directed as a quarantine method to prevent the establishment of the pink bollworm, Pectinophora gossypiella (Sanders), in the San Joaquin Valley of California. The sterile moths released each year since 1968 have apparently prevented the establishment of this pest in the San Joaquin Valley (LaChance 1983).

SIT and the Corn Earworm

The island of St. Croix was surveyed during the summer of 1967 for the occurrence of several lepidopteran pests and was considered suitable as a location in which an SIT trial could be conducted against the CEW (Snow et al. 1968, Snow et al. 1969). Efforts to eradicate the CEW from the island were initiated in 1968. Insects for release were reared in a facility at Tifton, Georgia, shipped to St. Croix as pupae, and irradiated with 32 krad as adults. This SIT trial was unsuccessful in its primary objective since eradication was never achieved. Insect production and shipment problems were largely responsible for the failure and finally caused the termination of this eradication attempt in September, 1968. In addition to the problems with production and shipping, many of the CEW received in St. Croix were of poor quality, exhibiting high mortality, low fecundity, and a high frequency of locking during mating of laboratory-reared males and native females (Snow et al. 1971). Although colonies of CEW have been developed with a greater degree of competitiveness (Young et al. 1975) and with more vigor (Young et al. 1976),

and techniques have been devised to select mature pupae for irradiation (Gross and Young 1978), no SIT trial has been conducted against the CEW since these improvements have been made.

Hybrid Sterility

Discovery in Lepidoptera and Initial Studies

Laster (1972) successfully produced progeny from a cross between female Heliothis subflexa (Guenee) and male H. virescens (F.). The females from this cross were fertile but the males were sterile. When hybrid females were backcrossed to H. virescens males, sterility persisted in the male progeny throughout successive backcross (BC) generations. BC females used in traps were as attractive as H. virescens females to native H. virescens males (Laster et al. 1978). Raulston et al. (1978) and Carpenter et al. (1979) reported that BC females were sexually attractive to native H. virescens males under field conditions and competed well with H. virescens females for mates. Models were developed to demonstrate the theoretical potential for suppressing H. virescens (Knipling and Klassen 1976, Laster et al. 1976, Parvin et al. 1976, Makela and Huettel 1979). As more information concerning the BC insects became available, additional models were developed which provided more confidence in the use of BC insects to suppress populations of H. virescens.

Pilot Test of Hybrid Sterility

The encouraging results from early studies of hybrid sterility convinced scientists there was a need to determine the technical feasibility for population management using BC insects. Consequently, in the fall of 1977 on St. Croix, U. S. Virgin Islands, a pilot test was

initiated with two objectives: (1) to infuse a measurable amount of BC sterility into the native H. virescens population and (2) to evaluate population levels following this infusion. During this test, BC frequencies reached 94% for all locations on the island and field-reared BC insects were considered as competitive as native H. virescens (Proshold 1983). Proshold et al. (1983) concluded that the feasibility of managing H. virescens by releasing BC insects would be limited by the cost of rearing and distributing the insects rather than the behavior or competitiveness of the BC insects.

Hybrid Sterility and H. zea

Currently, hybrid sterility is available only for the suppression of one lepidopteran species, H. virescens. Studies have been initiated to investigate the potential of developing hybrid sterility for the CEW. These experiments have attempted to cross H. armigera from Australia with the H. zea from the U.S.A. The results from these crosses are inconclusive. If hybrid sterility cannot be produced from these crosses, other species of Heliothis will be employed in this effort (Laster et al. 1985).

Genetic Basis for Hybrid Sterility

Many studies have been conducted to provide an understanding of the causes and effects of hybrid sterility (Proshold and LaChance 1974, Proshold et al. 1975, Richard et al. 1975, Goodpasture et al. 1980a, LaChance and Karpenko 1981, LaChance and Karpenko 1983). These studies have demonstrated that the sterile hybrid males and BC males produce abnormal eupyrene sperm and do not inseminate females. Although the morphological abnormalities, double-headed and double-tailed sperm in the

F_1 and BC_1 through BC_5 males were indicative of desynapsis of H. virescens and H. subflexa chromosomes, the sperm of males from later BC generations undergo normal meiosis but have abnormal mitochondria at various locations along the sperm tail (Goodpasture et al. 1980b, LaChance 1984). These studies suggest that a replicating cytoplasmic factor originating from H. subflexa females interacts with the H. virescens genetic material. Since the presence of a cytoplasmic symbiont does not appear to cause this sterility (LaChance and Karpenko 1981, 1983), it is probable that an H. virescens nuclear gene product(s) fails to function satisfactorily with an H. subflexa gene(s) or gene product(s) from the mitochondria in the cytoplasm of the BC sperm.

Inherited Sterility

Introduction

Inherited sterility occurs when insects receiving a substerilizing dose of radiation, chemosterilant, or a combination of both produce progeny that yield a greater incidence of sterile eggs than their parents. The dose administered to the insects can be adjusted so that treated insects are fully sterile when they intermate or F_1 progeny are partially to completely sterile. Delayed sterility, inherited partial sterility, partial sterility, and F_1 sterility are terms that are synonymous with inherited sterility.

Serebrovsky (1940) suggested that insect pests might be controlled specifically by releasing large numbers of individuals carrying chromosomal translocations which would result in inherited sterility. Proverbs (1962) demonstrated that a low dose of radiation would induce inherited sterility in the codling moth, L. pomonella. North (1975)

listed 14 species from seven different families of Lepidoptera in which inherited sterility had been induced. Inherited sterility has since been reported in many additional Lepidopteran species including Spodoptera littoralis Boisd. (Wakid and Hayo 1974), Bombyx mori (Sugai and Mirumachi 1973, Murakami 1976), Cadra cautella (Walker) (Brower and Tilton 1975), Ostrinia nubilalis (Hübner) (He-qin and Hong-shang 1980, Nabors and Pless 1981), and Spodoptera frugiperda (J. E. Smith) (Carpenter et al. 1983). LaChance (1983) suggested that inherited sterility can be induced in any lepidopteran species as well as hemipteran species with holokinetic chromosomes or chromosomes with diffuse centromeres. Examples of hemipteran species in which inherited sterility has been demonstrated are Gonocerus angulatus Goeze (Delrio and Cavalloro 1975), Rhodnius prolixus (Stal) (Maudlin 1976), Oncopeltus fasciatus (Dallas) (LaChance et al. 1970), and Nezara viridula (L.) (Dyby 1983).

Inherited sterility also has also been reported in other arthropods. Szentesi (1975) found sterile F_1 progeny when irradiated (10 krad) Acanthoscelides obtectus Say (Coleoptera: Bruchidae) males were crossed with normal females. Robinson and van Heemert (1975) induced a few translocations in the F_1 generation when Hylema antigua Meigen (Diptera: Anthomyiidae) were irradiated at 0.5 krad. Feldman (1975) demonstrated that a high percentage (up to 60.8%) of chromosomal rearrangements could be induced in the gametes of F_1 Tetranychus urticae Koch (Acari: Tetranychidae) when parents were irradiated with x-rays at 0.5 to 2 krad.

Genetic Basis

Cytogenetic studies of species with a single kinetochore per chromosome (monokinetic) indicate that dominant lethal mutations induced by radiation are expressed during early embryonic stages and usually during the first few cleavage divisions. These mutations are characterized by the presence of chromosomal bridges and fragments within the nuclei (Fahmy and Fahmy 1954, LaChance and Riemann 1964, von Borstel and Rekemeyer 1959, LaChance and Riemann 1973). Since lepidopteran species are holokinetic and the spindle fibers are attached along the entire length of the chromosomes, chromosome fragments are not lost but carried along from one division to the next. The ability to transmit chromosomal fragments from one generation to the next produces a mixture of viable and non-viable progeny (von Borstel and Rekemeyer 1959, North and Holt 1968, Bauer 1967, LaChance et al. 1970). LaChance (1983) states that heterozygosity for a single chromosome translocation produces individuals that are, on the average, 50% sterile while heterozygosity for more than one translocation would yield individuals that are 75 to 100% sterile.

The sterility expressed in moths irradiated with a substerilizing dose of radiation is based on different genetic events rather than the inherited sterility expressed in the F_1 and F_2 moths. The P_1 moths produce sperm and ova that have either dominant lethal mutations or chromosomal translocations. When these gametes unite with normal gametes, those bearing dominant lethal mutations produce inviable zygotes while those bearing chromosome translocations produce a reduced number of F_1 progeny that are partially or totally sterile. The partially sterile F_1 moths produce a reduced number of F_2 progeny which

carry some chromosome translocations (LaChance 1983). Thus, a population can be suppressed for several generations due to inherited sterility. However, acutely and chronically irradiated insect populations are able to recover to a near-normal reproductive capacity after a few generations even though high frequencies of recessive lethals and chromosomal abnormalities may be present (Wallace 1956, Sankaranarayanan 1964, Brower 1979). It is difficult to assess the role of these recessive lethals and chromosomal abnormalities since they are often carried as a concealed genetic load. Nevertheless, recessive lethals cause death to the individual in homozygous form and Sankaranarayanan (1966) reported that subvital genes affecting reproduction can cause a negative impact on a population on a long-term basis.

Induction of Inherited Sterility

North (1975) suggested that inherited sterility could be induced by any mutagen that is an effective chromosome breaker. Gamma radiation has been used most often in research because of the general availability of Cobalt-60 and Cesium-137 sources. Other forms of ionizing radiation also have been useful. Lea (1956) reported that fast neutrons are more efficient than X or gamma rays in breaking chromosomes, and Murakami et al. (1965) and Lightly (1971) demonstrated that neutrons were more efficient in inducing recessive lethals in insects. North (1975) stated that radiation with a high linear transfer (LET) such as neutrons, is more effective per unit of absorbed energy than gamma or x-rays in inducing inherited sterility and will probably produce a more competitive P_1 moth. North and Holt (1970) reported that a lower dose of radiation is required to achieve complete F_1 sterility in Trichoplusia

ni (Hübner) if fast neutrons are used rather than gamma radiation. In addition, when pupae were irradiated with neutrons (0 to 10 krad), eggs were produced that had a higher hatch rate, and the F_1 progeny were more sterile than that which was achieved when gamma radiation was used.

Chemosterilants have been used to induce inherited sterility. Stimmann (1971) administered topical applications of tepa [tris (1-aziridinyl) phosphine oxide] in acetone to 3-day-old male T. ni. Dose-dependent sterility and inherited sterility were observed in P_1 and F_1 moths, respectively.

Inherited sterility has been induced by irradiating all life stages of insects (Hough 1963, Cogburn et al. 1966, Hossain 1972, Debolt 1973, Nielson and Lambremont 1976). Generally, irradiation of stages prior to the late pupa has been unsatisfactory (Proverbs 1962, Godwin et al. 1965, Cogburn et al. 1966, Qureshi et al. 1967, 1970, Walker et al. 1971). Irradiation of embryos and larvae has resulted in high mortality, malformed adults, improper eclosion, and inability to mate. Since adults and pharate adults do not undergo metamorphosis, somatic damage is minimized when these forms are irradiated. Progeny from irradiated adults or late pupae exhibit equal amounts of inherited sterility (Cogburn et al. 1966, Walker et al. 1971, Debolt 1973, Nielson and Lambremont 1976).

Predictive Models

Knipling (1970) was the first to demonstrate the potential advantage of inherited sterility over SIT through the use of population

models. His initial models predicted that a population of four times as many sterile insects as insects irradiated with a substerilizing dose would be required to achieve equal suppression of a native population within three generations. Knipling suggested that the potential effect of persistent genetic suppressive action through several successive generations can easily be overlooked or remain obscure unless basic data on sterility in insects are evaluated in terms of practical use by a theoretical biomathematical model.

The basic rationale and methods Knipling (1970) used to develop his models guided other researchers to model data obtained from studies on inherited sterility. North and Holt (1969) calculated the theoretical depression of T. ni populations resulting from a single release of partially sterile males at a 1:1 or 9:1 ratio. They projected that 92% control could be obtained for three generations through the use of inherited sterility. Similar conclusions were expressed for Galleria mellonella (L.) (Nielsen and Brister 1980), Ephestia cautella (Walker) (Brower 1980), Plodia interpunctella (Hübner) (Brower 1981), and S. frugiperda (Carpenter et al. 1983). LaChance (1983) stated that all theoretical models comparing inherited sterility with SIT have demonstrated that inherited sterility is more effective in suppressing native populations than an equal number of fully sterile insects.

Field Trials on Inherited Sterility

The predictions of theoretical models concerning the relative effectiveness of inherited sterility and SIT have been validated by the results from several studies. Toba et al. (1972) compared sterile (30 krad) and partially sterile (15 krad) T. ni males for their ability to

suppress populations within large cages. The partially sterile males provided greater suppression (92% vs. 82%) over two generations. Proverbs et al. (1978) also compared inherited sterility with SIT by releasing irradiated Cydia pomonella (L.) moths in a large orchard in British Columbia. After one season of releases, the partially sterile moths had reduced the wild population by ca. 59% compared to 38% for the sterile moths. Charmillot et al. (1976) and Charmillot (1977) also studied the use of inherited sterility to reduce populations of C. pomonella and found that suppression of the native population was very good. Several field tests of inherited sterility have been conducted against the gypsy moth, Porthetria dispar. These efforts are still under evaluation (Mastro and O'Dell, personal communication).

Inherited Sterility in the Corn Earworm

North and Holt (1970) induced inherited sterility in the CEW by irradiating males with a 20-krad dose and mating them with normal females. The percent egg hatch of eggs from this cross was 36% compared to 77.9% for eggs from a normal female X normal male cross. The progeny from the irradiated males were outcrossed to normal moths and a higher incidence of sterility was observed than for the parental cross. In both the normal female X F_1 male cross and the F_1 female X normal male cross, the average number of eggs per female did not differ from the control.

The largest single drawback in the use of irradiated male moths to suppress natural populations has been considered the lack of competitiveness primarily due to the inability of irradiated males to transfer sperm successfully (North and Holt 1971). North and Holt

(1970) reported a study in which all CEW males that mated transferred a normal ratio of eupyrene:apyrene sperm. This was true even when CEW males were exposed to a 25-krad dose of radiation. Snow et al. (1972) found that the quantity and quality of sperm transferred to CEW females were reduced when males were irradiated with 17.5 and 35 krad, but less deviation from normality was found at the lower dose. Also, they reported that CEW females that had mated with males treated with 17.5 or 35 krad were as attractive as virgin females the night following copulation, whereas females that had mated with normal males were significantly less attractive.

North and Holt (1971) concluded that the CEW is an ideal candidate for using inherited sterility for population suppression. Knipling (1979) also cited the CEW as a potential candidate for the use of inherited sterility and projected the economic benefit that might be realized through such a program. LaChance (1983) recommended that the CEW be considered as a potential candidate to be controlled by genetic methods with emphasis on inherited sterility. He also emphasized the need to acquire the necessary technology for the employment of inherited sterility or another genetic control method against the CEW and other major lepidopteran pests.

CHAPTER THREE
INHERITANCE OF RADIATION-INDUCED DELETERIOUS EFFECTS

Materials and Methods

The CEW (Figures 1 and 2) used in this study were taken from the laboratory colony at the Insect Biology and Population Management Research Laboratory, Tifton, Georgia, which has been maintained as a laboratory colony for 200+ generations. All CEW were reared in 30 ml plastic cups containing meridic diet (Burton 1969). The photoperiod regime was 14:10 LD at a temperature of 29 $\pm$ 1°C and 24 $\pm$ 1°C, respectively. Relative humidity was maintained at ca. 70% within the environmental chamber (Percival®, model I60LV). All irradiation was done in a nitrogen atmosphere at ca. 20°C with a well-type ^{60}Co source (Gammarad Irradiator®, model GR-12) (Figure 3) delivering ca. 1.0 krad/min. Dose calibration using Fricke dosimetry indicated a dose error of ca. $\pm$ 5%.

This study consisted of four different trials. In the first trial, newly emerged CEW (1 to 12-h-old) males and females were irradiated with 0, 2, 4, 6, 8, 10 and 12 krad of gamma radiation. Treated (T) males were paired with normal (N) females and T females with N males. In the second trial, male and female adults (1 to 12-h-old) were irradiated with a 10-krad dose. These adults were paired (TxT) and outcrossed with N adults (TxN, NxT). An NxN cross served as the control. All possible crosses of F_1 and F_2 adults were made according to the number of surviving adults in each line. In addition to these crosses, F_1 and F_2 adults from selected lines were backcrossed to irradiated (10 krad)

P_1 adults. The crossing scheme for this trial is illustrated as follows:

N = normal

T = treated with 10 krad

(female x male)

P_1 crosses (F_1)	NxN (1), NxT (2)
	TxN, TxT
F_1 crosses (F_2)	1x1 (A), 2x1 (B), 1x2 (C)
	2x2, 1xT, txl
	2xT, Tx2
F_2 crosses	AxA, AxB, AxC
	BxA, BxB, BxC
	CxA, CxB, CxC
	AxT, TxA, BxT
	TxB, CxT, TxC

In the third trial, irradiated pupae (24 h before eclosion) and irradiated adults (1 to 24-h-old) were compared. Males from each treatment were outcrossed and inbred. An NxN cross was used as a control for each generation. The crossing scheme for the third trial was as follows:

N = normal

T_A = adults treated with 10 krad

Tp = pharate adults treated with 10 krad

P_1 crosses (F_1)	NxN,(N), NxT_A (A)
	NxTp (P)
F_1 crosses	NxN, NxA, AxN
	PxN, NxP, PxP
	AxA

In the fourth trial, male and female adults (1 to 24-h-old) were irradiated with 0, 12, 18, 21, 24, and 27 krad doses. T males and T females were inbred and T males were outcrossed to N females. Progeny from each F_1 cross were inbred.

For each cross, five pairs of moths were placed in each of ten 3.8-liter containers for mating and oviposition (five containers per F_2 cross). Beer was provided as a food source. The top of each cage was covered with 27 by 27 cm paper toweling on which eggs could be oviposited. After 5 days, the females were dissected to determine their mating status by counting the number of spermatophores in the bursa copulatrix. Each day, eggs were counted to determine the relative fecundity of females from the different crosses. One hundred eggs from each cross were held for 5 days to calculate the percentage of hatch. First instar larvae from each cross were placed on meridic diet (one larva per cup) and allowed to complete their development. Survival of insects and the resulting sex ratio were recorded. In all cases, treatments were subjected to analysis of variance and differences between means were tested for significance ($P < 0.05$) using Duncan's multiple range test (SAS 1982).

Results

The number of adult females produced from irradiated males outcrossed to normal females was dose-dependent (Table 1); however, the components of reproduction (egg hatch, eggs per female, larval survival, sex ratio) that influenced production of females responded differently to the radiation treatments. The number of eggs per female and the number of spermatophores per mated female did not exhibit a dose response

and were not significantly different from the control. A dose response was demonstrated by egg hatch, larval survival, and sex ratio. The number of larvae surviving to adult stage was the best single indicator of the total amount of radiation-induced deleterious effects demonstrated during this generation.

The production of female adults and all components of reproduction listed in Table 2 for irradiated female outcrosses demonstrated a strong dose response to the radiation treatments. The percent egg hatch had the greatest effect upon the number of females produced by these crosses. Significant differences between radiation doses were evidenced for all components of reproduction. The number of spermatophores per mated female was not influenced significantly by the radiation treatments.

The type of radiation-induced deleterious effects was similar both for outcrossed pairs (NxT, TxN) and for inbred pairs (TxT) (Table 3). In each of these crosses, the decrease in production of F_1 female adults resulted largely from significant ($\underline{P} < 0.05$) reductions in egg hatch and larval-pupal survival. Female adult production was lowest in crosses involving irradiated females. These data concerning female adult production support the data presented in Tables 1 and 2.

Only progeny from the P_1 NxN and NxT crosses were used in making the F_1 crosses since reproduction from the P_1 TxN and TxT crosses was so low and the number of crosses in each generation was limited by labor and facilities. The inherited deleterious effects in the F_1 generations were evidenced most strongly by significant ($\underline{P} < 0.05$) reductions in egg hatch and larval-pupal survival (Table 3). These deleterious effects had their greatest expression when P_1 NxT progeny

were inbred (2x2). Outcrosses of P_1 NxT progeny (1x2, 2x1) were not significantly ($P < 0.05$) different in any component of reproduction. Each of the F_1 crosses involving progeny from the P_1 NxT cross exhibited lower reproductive capabilities than those of the parental crosses.

Significant ($P < 0.05$) reductions in egg hatch and larval-pupal survival were recorded in the F_2 generation, indicating that recessive lethals were still present in the population (Table 3). However, recovery from the adverse effects of the radiation treatment was evident since the production of female adults was higher in the F_2 inbred crosses than in the parental crosses. Inherited deleterious effects had their greatest expression in the sibling cross of progeny from the N female x(P_1 NxT) male cross (BxB).

Progeny from the P_1 NxT cross which were backcrossed to irradiated (10 krad) adults produced fewer adult females than when these same adults were outcrossed to normal adults (e.g., 2xT and Tx2 compared with 1x2, 2x1, 1xT and Tx1) (Table 4). Again, F_1 adults (from P_1 NxT cross) oviposited a greater percentage of sterile eggs and produced fewer adult females than P_1 irradiated adults (2x1 and 1x2 compared to Tx1 and 1xT) which supports the data presented in Table 3. Significant ($P < 0.05$) expressions of deleterious effects reported for the F_2 generation were similar to those reported for the F_1 generation. Crosses between N female x(P_1 NxT) male progeny and irradiated adults (e.g., TxB, BxT, TxC, CxT) produced fewer adult females than when those individuals were outcrossed to normal adults (e.g., AxT, TxA, AxB, BxA, AxC, CxA).

Pharate and ca. 12-h-old males responded similarly to a 10-krad dose of radiation (Table 5) when outcrossed to normal females. No significant ($P < 0.05$) differences were found between the two crosses for the number of eggs oviposited, eggs hatched, larvae surviving to the adult stage, and the sex ratio. The progeny produced from irradiated pharate males exhibited similar levels of inherited deleterious effects as the progeny from the irradiated 12-h-old male.

Doses of radiation ranging from 12 krad to 27 krad significantly ($P < 0.05$) reduced the number of eggs oviposited, egg hatch, the number of spermatophores per mated female, the larval-pupal survival and the percent female progeny when irradiated males were outcrossed to normal females (Table 6). The progeny from these crosses were inbred and eggs produced were collected. Part of the eggs were used in an egg hatch study while the remaining eggs were pooled by treatment and held for hatch. No eggs hatched in the standard egg hatch study, but nine eggs hatched from the eggs bulked for the 15 krad F_2 inbred cross. Only two of these larvae produced viable adults. Inbred crosses involving CEW irradiated with different doses of radiation (12-27 krad) produced only a few F_1 adults (Table 7). No viable progeny were produced when these F_1 adults were inbred.

Table 1.--Effects of gamma irradiation of male corn earworm adults on reproduction of P_1 adults (P_1 adults irradiated ca. 12 h after emergence)[a/]

Dose of irradiation (krad)	Crosses (♀ x ♂)[b/]	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	Larvae surviving to adult (% of control)[c/]	Percent female	Production of ♀ adults (% of control)[d/]
0 (control)	NxN	100 ab	100 a	1.5 a	100 a	48 a	100
2	NxT	116 a	92 ab	2.0 a	91 a	43 ab	91
4	NxT	89 b	81 ab	1.8 a	101 a	50 a	77
6	NxT	88 b	94 ab	1.6 a	83 ab	48 a	73
8	NxT	92 b	96 a	1.8 a	71 b	40 ab	51
10	NxT	108 ab	77 ab	1.7 a	76 b	31 b	43
12	NxT	113 a	68 b	1.8 a	49 c	36 b	28

[a/] Means followed by the same letter are not significantly different at 5% level, Duncan's multiple range test (SAS 1982).
[b/] N = Normal; T = Treated.
[c/] 100 larvae per cross were placed on meridic diet.
[d/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

Table 2.--Effects of gamma irradiation of female corn earworm adults on reproduction of P_1 adults (P_1 adults irradiated ca. 12 h after emergence)[a/]

Dose of irradiation (krad)	Crosses (♀ x ♂)[b/]	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	Larvae surviving to adult (% of control)[c/]	Percent female	Production of ♀ adults (% of control)[d/]
0 (control)	NxN	100 a	100 a	1.7 a	100 a	56 a	100
2	TxN	102 a	87 a	1.8 a	93 a	52 a	64
4	TxN	100 a	35 b	2.0 a	60 b	36 b	11
6	TxN	93 ab	11 c	1.8 a	40 c	28 c	2
8	TxN	92 ab	7 c	1.6 a	18 d	38 b	1
10	TxN	82 bc	5 c	1.6 a	41 c	43 ab	1
12	TxN	77 c	8 c	1.7 a	51 bc	36 b	2

[a/] Means followed by the same letter are not significantly different at 5% level, Duncan's multiple range test (SAS 1982).
[b/] N = Normal; T = Treated.
[c/] 100 larvae per cross were placed on meridic diet.
[d/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

Table 3.--Effects of gamma irradiation of corn earworm adults on reproduction of P_1, F_1, and F_2 adults (P_1 adults irradiated with 10 krad ca. 12 h after emergence)[a/]

Crosses (♀ x ♂)	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	No. larvae placed on diet	Larvae surviving to adult (% of control)	Percent female	Production of ♀ adults (% of control)[b/]
P_1 Crosses[c/]							
NxN(control)	100 a	100 a	2.8 a	400	100 a	60 a	100
NxT	99 a	64 b	2.6 a	800	84 a	45 ab	42
TxN	97 a	8 c	2.2 a	300	33 b	42 b	2
TxT	97 a	7 c	2.6 a	200	28 b	55 a	2
F_1 Crosses[d/]							
1x1(control)	100 a	100 a	1.8 a	828	100 a	45 a	100
1x2	94 bc	52 b	1.8 a	828	45 b	42 a	20
2x1	98 ab	66 b	1.6 a	828	46 b	52 a	35
2x2	91 c	9 c	1.8 a	112	9 c	22 b	0.4
F_2 Crosses[e/]							
AxA(control)	100 a	100 a	1.6 a	300	100 a	50 a	100
BxA	95 a	81 ab	1.8 a	300	93 a	48 a	70
CxA	93 a	79 ab	1.5 a	300	85 ab	45 a	59
AxB	101 a	62 b	1.8 a	300	98 a	50 a	63

Table 3--continued

Crosses (♀ x ♂)	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	No. larvae placed on diet	Larvae surviving to adult (% of control)	Percent female	Production of ♀ adults (% of control)[b/]
BxB	94 a	55 b	1.4 a	300	75 b	42 a	33
CxB	96 a	66 b	1.4 a	300	84 ab	48 a	52
AxC	103 a	66 b	1.8 a	300	90 ab	50	62
BxC	94 a	69 b	1.4 a	300	80 b	48 a	51
CxC	98 a	98 a	1.5 a	300	58 c	48 a	43

[a/] Means followed by the same letter in each column in each generation are not significantly different at 5% level, Duncan's multiple range test (SAS 1982).
[b/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.
[c/] N = Normal; T = Treated.
[d/] 1 = progeny from P_1 NxN; 2 = progeny for P_1 NxT.
[e/] A = progeny from F_1 1x1; B = progeny from F_1 2x1; C = progeny from F_1 1x2.

Table 4.—Effects of gamma irradiation on H. zea reproduction when descendants from irradiated P_1 adults are backcrossed to P_1 adults (adults irradiated with 10 krad ca. 12 h after emergence)[a/]

Crosses (♀ x ♂)	Fecundity (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	No. larvae placed on diet	Larvae surviving to adult (% of control)	Percent female	Production of ♀ adults (% of control)[b/]
F_1 Crosses[c/]							
1x1(control)	100 ab	100 a	1.8 a	100	100 a	55 ab	100
2x1	88 b	46 c	1.8 a	100	41 bc	47 bc	14
1x2	78 b	51 bc	1.5 a	100	71 ab	42 bc	21
Tx1	71 b	64 abc	1.8 a	100	43 bc	72 a	25
1xT	132 a	88 ab	1.6 a	100	64 b	44 bc	59
Tx2	77 b	33 c	1.7 a	100	14 d	31 c	2
2xT	79 b	65 abc	1.4 a	30	22 cd	33 bc	7
F_2 Crosses[d/]							
AxA(control)	100 a	100 a	1.7 ab	100	100 ab	44 ab	100
BxA	98 a	69 abc	1.3 b	100	100 ab	47 ab	72
CxA	99 a	58 bcde	1.8 ab	100	108 ab	44 ab	62

Table 4--continued

Crosses (♀ x ♂)	Fecundity (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	No. larvae placed on diet	Larvae surviving to adult (% of control)	Percent female	Production of ♀ adults (% of control)[b/]
AxB	103 a	68 abc	2.1 a	100	127 a	36 ab	73
AxC	98 a	72 ab	1.9 ab	100	119 a	33 b	63
TxA	96 a	30 def	1.3 b	100	29 c	50 a	10
AxT	95 a	61 bcd	1.4 ab	100	84 b	36 ab	40
BxT	94 a	28 ef	1.3 b	100	95 ab	50 a	29
TxB	98 a	14 f	1.5 ab	100	22 c	36 ab	2
CxT	93 a	38 cdef	1.5 ab	100	100 ab	39 ab	31
TxC	96 a	7 f	1.8 ab	100	37 c	35 b	2

[a/] Means followed by the same letter in each column in each generation are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).

[b/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

[c/] 1 = normal; 2 = progeny from P_1 normal female x treated male; T = P_1 treated (10 krad).

[d/] A = normal; B = progeny from F_1 2x1; C = progeny from F_1 1x2; T = P_1 treated (10 krad).

Table 5.--Effects of gamma irradiation on reproduction of P_1 and F_1 adults when H. zea are irradiated as pharate adults (mature pupae) and 12-h-old adults[a/]

Crosses (♀ x ♂)	Fecundity (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	No. larvae placed on diet	Larvae surviving to adult (% of control)	Percent female	Production of ♀ adults (% of control)[b/]
P_1 Crosses[c/]							
NxN	100 a	100 a	2.1 a	144	100 a	55 a	100
NxT_A	81 a	71 b	1.9 a	144	92 ab	43 a	43
NxT_p	89 a	89 ab	1.9 a	144	87 ab	43 a	53
F_1 Crosses[d/]							
NxN	100 ab	100 a	2.4 a	144	100 a	50 a	100
NxA	83 b	73 bc	1.7 b	144	82 b	50 a	50
AxN	111 a	76 b	1.9 ab	144	82 b	42 a	58
PxN	111 a	40 cde	1.9 ab	144	92 ab	45 a	36
NxP	100 ab	47 cd	2.2 ab	144	79 b	45 a	34
PxP	102 ab	29 de	2.1 ab	144	83 b	52 a	26
AxA	86 ab	18 e	1.9 ab	144	34 c	50 a	6

Table 5--continued

[a] Means followed by the same letter in each column in each generation are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).

[b] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

[c] N = normal; T_A = 12-h-old adults irradiated with 10 krad; T_p = mature pupae (pharate adults) irradiated with 10 krad.

[d] N = normal; A = progeny from P_1 NxT_A; P = progeny from P_1 NxT_p. (10 krad).

Table 6.--Response of H. zea to different doses of radiation when irradiated males (treated ca. 12 h after emergence) are outcrossed to normal females[a/]

Dose of irradiation (krad)	Crosses (♀ x ♂)	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	Larvae surviving to adult (% of control)[b/]	Percent female	Production of ♀ adults (% of control)[c/]
Control	NxN	100 a	100 a	1.46 ab	100 a	52 a	100
12	NxT	68 b	58 b	1.30 ab	68 b	34 bc	18
15	NxT	102 a	53 b	1.70 a	79 b	37 b	30
18	NxT	62 bc	28 c	1.42 ab	53 c	34 bc	6
21	NxT	71 b	26 c	1.30 bc	32 d	32 bc	4
24	NxT	48 cd	17 c	1.50 ab	32 d	21 c	1
27	NxT	45 d	12 c	1.10 c	24 d	6 d	0.1

[a/] Means followed by the same letter are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).

[b/] 100 larvae per cross were placed on meridic diet.

[c/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

Table 7.--Response of H. zea to different doses of radiation when irradiated adults (treated ca. 12 h after emergence) are inbred [a/]

Dose of irradiation (krad)	Crosses (♀ x ♂)	Eggs/♀ (% of control)	Egg hatch (% of control)	Spermatophores per mated ♀	Larvae surviving to adult (% of control)[b/]	Percent female	Production of ♀ adults (% of control)[c/]
Control	NxN	100 a	100 a	2.5 b	100 a	42 a	100
12	TxT	68 ab	70 b	2.6 b	52 b	45 a	26
15	TxT	79 ab	25 c	2.4 b	30 c	42 a	6
18	TxT	86 ab	22 cd	2.5 b	15 de	52 a	3
21	TxT	65 b	16 cd	2.7 b	22 cd	30 a	2
24	TxT	67 b	8 d	2.2 b	7 e	50 a	4
27	TxT	94 ab	10 d	3.3 c	16 d	45 a	2

[a/] Means followed by the same letter are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).

[b/] 144 larvae per cross were placed on meridic diet.

[c/] Values in this column are products of fecundity, egg hatch, survival, and sex ratio.

Figure 1.--Female Heliothis zea (Boddie) (Lepidoptera: Noctuidae) adult.

Figure 2.--Male Heliothis zea (Boddie) (Lepidoptera: Noctuidae) adult.

Figure 3.--Cobalt 60 Gammarad Irradiator (Model GR-12) located at the USDA-ARS Insect Biology and Population Management Research Laboratory, Tifton, Ga.

CHAPTER FOUR
FIELD SURVIVAL OF LARVAE FROM IRRADIATED PARENTS

Materials and Methods

Male and female CEW adults (see Chapter Three for rearing and irradiation methods) were inbred as normal adults (NxN), irradiated with a 10-krad dose and inbred (TxT), and outcrossed to normal adults (Nxt, TxN). In each of those four crosses, five pairs of moths were placed in each of ten 3.8-liter containers for mating and oviposition. Beer was provided as a food source, and the top of each cage was covered with 27 by 27 cm paper toweling on which eggs could be oviposited. The eggs were collected after 2 days of oviposition. Percentages of egg hatch and rates of survival were determined in the laboratory for each cross by the methods described in Chapter Three.

A field study was conducted on the Insect Biology and Population Management Research Laboratory experimental farm near Tifton, Georgia, in 1984. The experimental area was planted with 'Silver Queen' sweet corn in rows 0.48 m apart, and standard agronomic practices were employed. No pesticides were applied to the corn during the study. Plots consisted of one row, 9.0 m long, thinned to 15 plants and bordered by three rows. Two experiments were conducted simultaneously in which plots of each were arranged in a randomized complete block design and replicated six times. Late-whorl stage corn (Batchelder 1946) was infested with 5 eggs per plant in one experiment and 50 eggs per plant in the other. The eggs, which had been oviposited on paper toweling, were pinned deep within the whorl of each plant within each plot on 28 May.

Natural infestation levels were monitored by control plots which were not artificially infested. The number of plants per plot damaged by active larval feeding was recorded on 8 and 11 June. Plants also were dissected on 11 June, and 4th and 5th CEW instars were collected and placed on diet. Mortality and percent parasitism were recorded. All data were subjected to analysis of variance and differences between means were tested for significance ($P < 0.05$) using Duncan's multiple range test (SAS 1982).

Results

F_1 larvae (resulting from an infestation rate of 5 eggs per plant) from the NxN, NxT, and TxN crosses damaged significantly ($P < 0.05$) more plants on 8 June 1984 than larvae from the TxT cross or those present in the control plots (Table 8). The NxN, NxT, and TxN crosses remained significantly different from the control on 11 June; however, the TxN and TxT crosses were no longer significantly different from each other. The number of mature larvae collected from the infested corn exhibited the same relationship among the crosses as did the number of damaged plants, although the differences were not significant. Significantly more ($P < 0.05$) larvae were collected from the NxN and NxT plots than the control plots. The largest number of adults was produced from the NxN plots and the smallest number of adults was produced from the TxT plots; however, these differences were not significant (Table 8).

Significantly ($P < 0.05$) more plants were damaged by F_1 larvae from the NxN and NxT crosses than the TxN and TxT crosses, and larvae from the TxN and TxT crosses damaged significantly ($P < 0.05$) more plants than the larvae in the control plots when corn was infested at a

rate of 50 eggs per plant (Table 9). The number of mature larvae collected also demonstrated this relationship since crosses involving normal females produced significantly ($P < 0.05$) more adults than the other crosses. Crosses involving irradiated insects did not produce significantly more adults than the control (Table 9). The rate of parasitization was variable and no significant differences were observed (Tables 8, 9).

F_1 percent survival was higher for all crosses in the laboratory than under field conditions and higher in the field when the infestation rate was 5 eggs per plant than when it was 50 eggs per plant (Table 10). The survival for the NxN cross was significantly ($P < 0.05$) higher than the other crosses, and crosses involving irradiated females were significantly ($P < 0.05$) lower than the other crosses when reared in the laboratory. These differences between crosses were not as evident under field conditions. Relative field survival (% of NxN) for the TxN (75 and 44) and TxT (25 and 28) crosses was much higher than the relative laboratory survival of 2.6% and 2.0%, respectively. An estimation of the rate of increase from the P_1 to the F_1 generation of CEW reared in the laboratory and field was calculated from the data in Table 10 by assuming that one female produces 1,000 eggs and that sex ratios are 1:1 (Table 11). The rate of increase for NxN and NxT in the laboratory is very high (330 and 180, respectively), while the rate of increase for TxN and TxT is relatively low (8.5 and 6.5). Under field conditions at an infestation rate of 5 eggs per plant, the differences between the crosses are much less and each of the crosses exhibits a rate of increase near the fivefold level suggested by Knipling (1968). When

plants were infested with 50 eggs per plant, the estimated rate of population increase resulting from each cross was less than onefold, indicating that all of the crosses would experience a decline in their population levels under these rearing conditions.

Table 8.--Comparison of field survival between H. zea from normal and irradiated parents when sweet corn was infested with 5 eggs per plant[a/]

P_1 Crosses (♀ x ♂)[b/]	$\bar{x}$ plants damaged[c/] 8 June	11 June	$\bar{x}$ no. of mature larvae collected	$\bar{x}$ no. larvae parasitized[d/]	$\bar{x}$ no. adults produced from larvae
NxN	48.7 a	46.7 a	3.0 a	14.5 a	1.33 a
NxT	56.7 a	50.0 a	3.3 a	10.0 a	1.00 a
TxN	38.0 a	32.0 ab	2.2 ab	16.7 a	1.00 a
TxT	18.7 a	21.3 bc	1.2 ab	16.7 a	0.33 a
None (Control)	13.3 b	8.7 c	0.8 b	0 a	0.67 a

[a/] Means followed by the same letter are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).
[b/] N = Normal, T = Treated (10 krad).
[c/] Only plants with evidence of active larval feeding were counted.
[d/] Only the mature larvae collected were observed for parasitism.

Table 9.--Comparison of field survival between H. zea from normal and irradiated parents when sweet corn was infested with 50 eggs per plant[a/]

P_1 Crosses (♀ x ♂)[b/]	$\bar{x}$ plants damaged[c/] 8 June	11 June	$\bar{x}$ no. of mature larvae collected	$\bar{x}$ no. larvae parasitized[d/]	$\bar{x}$ no. adults produced from larvae
NxN	84.7 a	84.7 a	13.2 a	28.3 a	3.00 a
NxT	76.7 a	82.0 a	10.8 a	20.6 a	1.33 b
TxN	35.3 b	31.3 b	4.7 b	7.5 a	1.33 b
TxT	31.3 b	28.7 b	2.8 bc	25.0 a	0.83 b
None (Control)	5.3 c	8.7 c	1.3 c	33.3 a	0.83 b

[a/] Means followed by the same letter are not significantly different ($P < 0.05$, Duncan's multiple range test) (SAS 1982).
[b/] N = Normal, T = Treated (10 krad).
[c/] Only plants with evidence of active larval feeding were counted.
[d/] Only the mature larvae collected were observed for parasitism.

Table 10.--Comparison of field and laboratory survival between H. zea from normal and irradiated parents[a/]

P_1 Crosses (♀ x ♂)[b/]	% survival, egg to adult (% of NxN)		
	Laboratory	Field-5 eggs per plant	Field-50 eggs per plant
NxN	66 a (100)	1.77 a (100)	0.04 a (100)
NxT	36 b (55)	1.33 a (75)	0.018 b (44)
TxN	1.7 c (2.6)	1.33 a (75)	0.018 b (44)
TxT	1.3 c (2.0)	0.44 a (25)	0.011 b (28)

[a/] Means followed by the same letter are not significantly different ($P < 0.05$, multiple range test) (SAS 1982).

[b/] N = Normal, T = Treated (10 krad).

Table 11.--Estimated rate of increase from P_1 to F_1 generation for H. zea from normal and irradiated parents when reared under laboratory and field conditions[a/]

P_1 Crosses (♀ x ♂)[b/]	Laboratory: 1 larva/cup of diet	Field 5 eggs/plant	Field 50 eggs/plant
NxN	330	8.87	0.20
NxT	180	6.67	0.09
TxN	8.5	6.67	0.09
TxT	6.5	2.20	0.06

[a/] It is assumed that one female produces 1000 eggs and that sex ratios are 1:1.
[b/] N = Normal, T = Treated (10 krad).

CHAPTER FIVE
EFFECTS OF IONIZING RADIATION AND INHERITED STERILITY ON MATING COMPETITIVENESS

Materials and Methods

All CEW adults for these studies were reared and irradiated according to the methods described in Chapter Three.

Field Cage Studies

Four field cages (9 by 30 by 4.1 m, covered with Saran® screen) (Figure 4) were planted with cotton, Gossypium hirsutum L. (variety: 'Coker 310'). The cotton was thinned periodically to limit foliage density and facilitate nocturnal observations of insect behavior.

Irradiated and normal laboratory-reared moths were color-coded according to moth type and age by chilling the moths to 17 ± 1°C and marking the wing tips with a felt-tip marker. These moths were placed in 3.8 liter containers by sex with 10 moths per container and allowed to acclimate outside from 1700 h EST until they were released by sex in opposite ends of the cages at 2000 h EST. Two workers entered each cage once every hour for ca. 10 min to collect mating pairs and observe moth behavior. Hourly observations and collections were initiated at 2100 h EST and terminated at 0200 h EST the following morning. The moths remaining in the cages after each night were removed to maintain a controlled moth population.

Mating competitiveness of different moth types was determined by releasing the following moth combinations: (i) 10 pairs per cage of irradiated (10 krad) males and females released 5 h after irradiation and

10 pairs per cage of normal moths of the same age; (ii) 10 pairs per cage of irradiated (10 krad) males and females released 5 h after irradiation and 10 pairs per cage of normal moths of the same age; (iii) 10 pairs per cage of irradiated (35 krad) males and females released 30 h after irradiation and 10 pairs per cage of normal moths of the same age; (iv) 10 pairs per cage of irradiated (35 krad) males and females released 5 h after irradiation and 10 pairs per cage of normal moths of the same age; (v) 10 irradiated (10 krad) and mated males per cage released ca. 24 h after copulation and 10 pairs per cage of normal, virgin moths of the same age; (vi) 10 irradiated (10 krad) and mated males per cage released ca. 48 h after copulation and 10 pairs per cage of normal, virgin moths of the same age; (vii) 10 F_1 males per cage (progeny from irradiated (10 krad) male x normal female) and 10 normal males and 20 normal females per cage. Each of these combinations was replicated by cage for four nights. All data were subjected to analysis of variance and differences between means were tested for significance ($P < 0.05$) using Duncan's multiple range test (SAS 1982).

Field Studies 1983

Two areas (0.4 ha each) separated by ca. 0.8 km were planted with tobacco, Nicotiana tobacum L. A 75-50 cone trap (Hartstack et al. 1979) (Figure 5) baited with a synthetic sex lure was centrally located within each of the two areas. The synthetic lures were formulated by Herculite Products, Inc., New York, NY 10010, each consisting of 1.25 mg of the four-component CEW pheromone (Klun et al. 1980) contained in 1.3 x 2.5 cm laminated plastic.

CEW moths were marked and acclimated as described in the field cage studies. Each night at 2000 h EST for five nights, 50 pairs of normal

laboratory moths and 50 pairs of irradiated (10 krad) moths were released by sex in each of the two areas. Two workers in each area collected mating pairs and recorded the number and type of single moths observed for 50 min of each hour. Hourly observations and collections were initiated at 2100 h EST and terminated at 0200 h EST the following morning. The number and type of male CEW caught in each trap were recorded hourly. Wild female moths were captured and the number of spermatophores within the bursa copulatrix of each female was counted. Analysis of variance and Duncan's multiple range test (SAS 1982) were used to separate treatment differences.

Field Studies 1984

A 2-ha field in the corner of a 14.2 ha area of cultivated land was planted with cotton (variety: 'Coker 310') and managed with standard agronomic practices. This field was bordered on the south and east by a mixture of hardwoods and pasture, and bordered on the north and west by mature cowpeas and field corn, respectively. The flowering and fruiting cotton was the most attractive host available for CEW within a 2-km radius at the time bioassays were conducted.

The cotton field was divided into quadrants, and one 75-50 cone trap (Hartstack et al. 1979) was placed in the center of each quadrant. Two of the traps were baited with 48-h-old virgin females (five females per trap) while the other two traps were baited with the CEW sex pheromone (Herculite Products, Inc.). Virgin females were replaced daily and the pheromone baits were replaced every 10 days.

CEW moths were marked and acclimated as described in the field cage studies. Each night at 2000 h EST for five consecutive nights, 250

pairs of normal laboratory moths and 250 pairs of irradiated (10 krad) laboratory moths were released by sex at four release sites midway between the four cone traps. Three workers searched the cotton field hourly by following predetermined paths that would allow each worker to transverse the field twice during each hour. Mating pairs and the number and type of male CEW caught in each trap were recorded hourly. Single CEWs were identified and moth activities were recorded from 2100 to 2200 h EST during each night. All females captured (in copula) were dissected to determine the number of spermatophores in the bursa copulatrix. Hourly observations and collections were initiated at 2100 h EST and terminated at 0200 h EST the following morning. This study was conducted from 7-10 August 1984.

Another study was conducted from 13-16 August 1984. This study used the same methods and materials as the first study except no females were released, and males were held 24 h after radiation treatment before being released. Data from both studies were subjected to analysis of variance and differences between means were tested for significance using Duncan's multiple range test (SAS 1982).

Results

Field Cage Studies

Laboratory-reared male and female moths irradiated with 10 krad were equally competitive with normal laboratory-reared moths in finding/luring and securing mates (Table 12). The time interval between irradiation and release of moths produced no measurable effect on mating competitiveness. Moths irradiated with 35 krad also were competitive with normal moths when released 30 h after the radiation treatment.

Irradiated (35 krad) moths released 5 h after the radiation treatment appeared to be less competitive. Significantly ($P < 0.05$) fewer mating pairs involving irradiated females (TxN, TxT) were collected than NxN mating pairs. The competitiveness of irradiated (10 krad) males was not altered by a previous mating experience or by the time interval between copulation and release of the irradiated males. F_1 males (progeny from irradiated (10 krad) males x normal females) were equally competitive with normal males in finding and securing mates.

Field Studies 1983

The nocturnal behavior of irradiated (10 krad) and normal laboratory-reared males was similar when released in 0.4 ha tobacco fields (Table 13). No significant ($P < 0.05$) differences were detected between normal and irradiated males for the number of matings, singles observed, or males captured in pheromone traps. Also, irradiated females demonstrated the same nocturnal behavior and mating competitiveness as normal females.

A comparison of the nocturnal behavior of wild and laboratory males indicated that the ratio of wild-to-laboratory was similar for the number of singles observed and the number of males captured in pheromone traps (Table 14) with the wild males constituting the larger number. This ratio was reversed for the number of mating pairs since most matings involved a laboratory male.

Field Studies 1984

Irradiated (10 krad) and normal laboratory-reared females exhibited similar nocturnal behavior and mating competitiveness when released in a 2-ha cotton field (Table 15). These females were not significantly

($P < 0.05$) different in their ability to lure and secure a mate or in the number of each type of female present within the field. Also, no significant ($P < 0.05$) differences were found between normal and irradiated (10 krad) males for the number of matings, singles observed, or males captured in traps (Table 16). Normal and irradiated males released in a 2-ha cotton field in the absence of laboratory-reared females also were not significantly different in their nocturnal behavior and mating competitiveness (Table 17).

A comparison of the nocturnal activity of wild and laboratory-reared males indicated that the ratio of wild-to-laboratory males was similar for the number of matings, number of singles observed, and number of males caught in traps (Table 18). The wild-to-laboratory male ratio was similar whether males and females were released or only laboratory males were released.

Table 12.--Mating competitiveness of H. zea moths treated (T) with gamma radiation vs. normal (N) moths in 9 by 30 m screened field cages

Type of moths[a/] released	$\bar{x}$ number of mating pairs collected[b/] NxN	NxT	TxN	TxT
10 krad male and female released 30 h after irradiation	2.4 a	2.8 a	2.7 a	2.3 a
10 krad male and female released 5 h after irradiation	2.3 a	2.7 a	2.7 a	2.4 a
35 krad male and female released 30 h after irradiation	2.4 a	2.6 a	2.3 a	2.7 a
35 krad male and female relased 5 h after irradiation	2.1 a	1.4 ab	1.2 b	0.9 b
10 krad mated male released 24 h after copulation	2.7 a	2.3 a	--	--
10 krad mated male released 48 h after copulation	2.8 a	2.8 a	--	--
F_1 male from 10 krad T male x N female cross	5.3 a	6.3 a	--	--

a/ Also released with these treated moths were normal virgin moths (same number, sex, and age). Normal female moths were released even if treated female moths were not.

b/ Means followed by the same letter in each row are not significantly different at the 5% level, Duncan's multiple range test.

Table 13.--Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared males when released in each of two 0.4-ha areas planted with tobacco[a/]

Type of male	$\bar{x}$ no. of matings per night	$\bar{x}$ no. of singles observed per night	$\bar{x}$ no. of males captured per night[b/]
North area			
Normal	7.4	4.8	9.8
Irradiated	7.6	2.3	6.3
South area			
Normal	7.8	0.3	8.5
Irradiated	5.8	1.0	8.0

[a/] Differences between means in the same column in the same area are not significant, $P = 0.05$, Duncan's multiple range test (SAS 1982).

[b/] Trap capture is for one cone trap (baited with synthetic pheromone) per area.

Table 14.--Comparison of the nocturnal behavior of wild and laboratory-reared (irradiated and normal) H. zea males in each of two 0.4-ha areas planted with tobacco[a/]

Type of male	$\bar{x}$ no. of matings per night (% of matings)	$\bar{x}$ no. of singles (% of singles)	$\bar{x}$ no. males captured per night (% of males captured)[b/]
North area			
Wild	9.4 (39)	16.3 (70)	131.0 (89)
Lab	15.0 (61)	7.1 (30)	16.0 (11)
South area			
Wild	13.2 (47)	16.3 (93)	177.0 (91)
Lab	14.6 (53)	1.3 (7)	16.5 (9)

[a/] 50 normal and 50 irradiated (10 krad) pairs of laboratory-reared moths of the same age were released 5 h after radiation treatment in each area each night.
[b/] Trap capture is for one cone trap (baited with synthetic pheromone) per area.

Table 15.--Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared females when released in a 2-ha cotton field[a/]

Type of female	$\bar{x}$ no. of matings per night	$\bar{x}$ no. of singles 2100-2200 h EST
Normal	53.3	5.3
Irradiated	52.0	3.8

[a/] Differences between means in the same column are not significant, $P = 0.05$, Duncan's multiple range test (SAS 1982).

Table 16.--Nocturnal behavior of normal and irradiated (10 krad, released 5 h after treatment) H. zea laboratory-reared females when released in a 2-ha cotton field[a/]

Type of male	$\bar{x}$ no. of matings per night	$\bar{x}$ no. of singles 2100-2200 h EST	$\bar{x}$ no. males captured per night[b/]
Normal	8.0	1.8	24.3
Irradiated	4.8	2.5	21.8

[a/] Differences between means in the same column are not significant, $P = 0.05$, Duncan's multiple range test (SAS 1982).

[b/] Trap capture is a total of two pheromone-baited cone traps and two virgin female-baited cone traps.

Table 17.--Nocturnal behavior of normal and irradiated (10 krad, released 30 h after treatment) H. zea laboratory-reared males when released in a 2-ha cotton field[a/]

Type of male	$\bar{x}$ no. matings per ings per night	$\bar{x}$ no. of singles 2100-2200 h EST	$\bar{x}$ no. males captured per night[b/]
Normal	0.5	1.5	25.5
Irradiated	1.8	3.5	24.0

[a/] Differences between means in the same column are not significant, $P = 0.05$, Duncan's multiple range test (SAS 1982).

[b/] Trap capture is a total of two pheromone-baited cone traps and two virgin female-baited cone traps.

Table 18.--Comparison of the nocturnal behavior of wild and laboratory-reared (irradiated and normal) H. zea males in a 2-ha cotton field

	2100-2200 h EST		
Type of male	$\bar{x}$ no. of matings per night (% of matings)	$\bar{x}$ no. of singles (% of singles)	$\bar{x}$ no. males captured[a] per night (% of males captured)
Male and female laboratory-reared moths released[b]			
Wild	96 (88)	9.8 (70)	129 (87)
Lab	13 (12)	4.3 (30)	19 (13)
Only male laboratory-reared moths released[c]			
Wild	55.3 (96)	39 (89)	240 (87)
Lab	2.3 (4)	5 (11)	36 (13)

[a] Trap capture is a total of two pheromone-baited cone traps and two virgin female-baited cone traps.

[b] 250 normal pairs and 250 irradiated (10 krad) pairs of the same age released 30 h after radiation treatment.

[c] 250 normal males and 250 irradiated (10 krad) males of the same age released 30 h after radiation treatment.

Figure 4.--Screened field cages (9 x 30 x 4.1 m covered with Saran® screen) used in mating propensity studies.

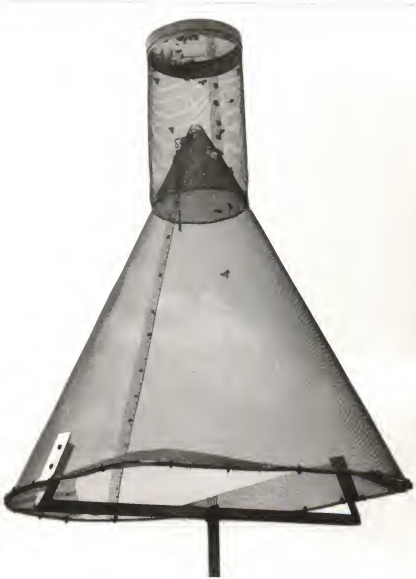

Figure 5.--Cone-75-50 trap (Hartstack et al. 1979) baited with Heliothis zea female sex pheromone.

CHAPTER SIX
MATING PROPENSITY OF FEMALES WITH DIFFERENT MATING HISTORIES

Materials and Methods

Trapping Study

Five 50-25 cone traps (Hartstack et al. 1979) were spaced 30 m apart (in a north-south line) at each of four locations on the 23-ha Insect Biology and Population Management Research Laboratory experimental farm. Locations 1 and 2 were surrounded by corn; location 3 was adjacent to corn and tobacco; and location 4 was adjacent to corn and sorghum. Each test night was treated as a replicate. Significance of differences was determined by analysis of variance and Duncan's multiple range test (SAS 1982).

Five baits were used in each of two trials. In the first trial the baits were virgin CEW females and CEW females with the following mating histories: (i) mated once to a normal male and held for 24 h; (ii) mated once to an normal male and held for 48 h; (iii) mated once to an irradiated (10 krad) male and held for 24 h; (iv) mated once to an irradiated (10 krad) male and held for 48 h. The female baits contained four females per bait. Each of the five baits was positioned in each of the four locations. The traps in each location were serviced and randomized daily. Females used as bait were dissected and the number of spermatophores in the bursa copulatrix was counted to verify the mating status. This trial was conducted from 12-17 July 1984.

Methods and materials for the second trial were the same as for the first trial except females were mated to F_1 males (progeny from irradiated (10 krad) male x normal female) instead of irradiated males. This trial was conducted from 21-27 July 1984.

Field Cage Study

Three field cages (9 by 30 by 4.1 m, covered with Saran® screen) were planted with sweet corn (variety 'Silver Queen'). Ten females mated once to normal males and held for 24 h, 10 females mated once to irradiated (10 krad) males and held for 24 h, and 20 normal males were marked, released in each of the three cages and bioassayed according to the methods described in Chapter Five. This trial was conducted from 11-15 July 1984. A second trial was conducted from 28-29 August and from 3-4 September 1984. Methods and materials for this trial were the same as for the first except females were mated to F_1 males (progeny from irradiated (10 krad) male x normal female) instead of irradiated males. In each trial, means were tested for significance by using analysis of variance and Duncan's multiple range test (SAS 1982).

Results

Trapping Study

Female CEW that had mated with normal and irradiated (10 krad) males and then held for 24 h were not significantly ($P < 0.05$) different in their attractiveness to males (Table 19). However, these females (mated + 24 hr) were significantly ($P < 0.05$) less attractive than virgin females or mated females held 48 h after mating. Females that had mated with normal males and then held for 48 h were not significantly ($P < 0.05$) different from virgin females or females that had mated with irradiated (10 krad) males and then held for 48 h (Table 19).

The attractiveness of females that had mated with F_1 males (progeny from irradiated (10 krad) male x normal female) and held for 24 h was significantly ($P < 0.05$) greater than the attractiveness of females that had mated to normal males and held for 24 h (Table 20). Again, females mated to normal males were significantly ($P < 0.05$) more attractive 48 h after mating than 24 h after mating. No significant differences were observed between the attractiveness of F_1 mated females 24 and 48 h after mating. Mated females held for 48 h after mating were not significantly ($P < 0.05$) different from virgin females in their attractiveness to males (Table 20).

Field Cage Study.

The mating propensity of females with different mating histories supported the data from the trapping study. Females that had mated with normal or irradiated (10 krad) males and held for 24 h were not significantly ($P < 0.05$) different in their ability to secure a second mate (Table 21). Females that had mated with F_1 males and held for 24 h secured significantly more mates than females that had mated with normal males and held for 24 h (Table 22).

Table 19.--Attractiveness of virgin females, females mated to normal males, and females mated to irradiated males in luring H. zea to traps

Type of female lure	$\bar{x}$ no. of males captured per trap per night[a/]
Virgin	76.3 a
Mated to irradiated male + 48 h	66.2 a
Mated to normal male + 48 h	56.7 a
Mated to irradiated male + 24 h	31.3 b
Mated to normal male + 24 h	25.3 b

a/ Means followed by the same letter are not significantly different, $P < 0.05$, Duncan's multiple range test (SAS 1982).

Table 20.—Attractiveness of virgin females, females mated to F_1 males (progeny from irradiated (10 krad) male x normal female), and females mated to normal males in luring *H. zea* males to traps.

Type of female lure	$\bar{x}$ no. of males captured per trap per night[a/]
Virgin	164 a
Mated to F_1 male at 48 h	149 a
Mated to normal male + 48 h	143 a
Mated to F_1 male + 24 h	124 a
Mated to normal male + 24 h	55 b

a/ Means followed by the same letter are not significantly different, $P < 0.05$, Duncan's multiple range test (SAS 1982).

Table 21.--Comparison of mating propensity of H. zea females mated once to normal males and held for 24 h, and H. zea females mated once to irradiated (10 krad) males and held for 24 h[a/]

Type of female	$\bar{x}$ no. ± matings per cage per night[b/]
Mated to irradiated male + 24 h	2.4 ± 1.5 a
Mated to normal male + 24 h	1.9 ± 1.2 a

[a/] Ten females of each type and 20 normal males per cage.
[b/] Means followed by the same letter are not significantly different, $P < 0.05$, Duncan's multiple range test (SAS 1982).

Table 22.--Comparison of mating propensity of H. zea females mated once to normal males and held for 24 h, and H. zea females mated once to F_1 males (progeny from irradiated (10 krad) male x normal female) and held for 24 h[a/]

Type of female	$\bar{x}$ no. ± matings per cage per night[b/]
Mated to F_1 male + 24 h	4.0 ± 1.3 a
Mated to normal male + 24 h	2.4 ± 1.6 b

a/ Ten females of each type and 20 normal males per cage.
b/ Means followed by the same letter are not significantly different, $P < 0.05$, Duncan's multiple range test (SAS 1982).

CHAPTER SEVEN
DISCUSSION

Effects of Radiation and Inherited Sterility on Reproduction

The effects of radiation and inherited sterility on the reproduction of CEW are similar to those of other species of Lepidoptera. LaChance (1983) stated that the two attributes of inherited sterility found in all species examined when irradiated males are mated with normal females are (1) a higher degree of sterility in the F_1 progeny than in the P_1 adults and (2) a skewed sex ratio of the F_1 favoring male progeny. Both of these attributes are demonstrated by the results from this research, although the skewed sex ratio plays a limited role in reducing the reproductive potential of CEW. For example, the sex ratio (percent female) resulting from the F_1 2x2 cross (Table 3) is significantly ($P < 0.05$) less (23%) than that from the F_1 1x1 (control) cross, and the production of female adults for 2x2 is 0.4% normal. However, if the sex ratio from the 2x2 cross were equal to the 1x1 sex ratio, the production of female adults for 2x2 would only be increased to 0.7% normal.

Brower (1975), North (1975), and Carpenter et al. (1983) report that the deleterious effects of radiation on the reproductive potential of several species are greater for females than for males. CEW females also demonstrate less radioresistance, especially in the range of 4-15 krad. North and Holt (1969) and LaChance (1983) suggest that the sensitivity differential between males and females may be an advantage if a

single dose of radiation would partially sterilize males and completely sterilize females.

Field Survival of Larvae From Irradiated Parents

The data reported in Chapter Three suggest that CEW populations may be controlled by releasing moths irradiated with substerilizing doses of radiation. Such a control method would require an understanding of the field survival and field competitiveness of larval descendants of irradiated parents. It is especially important to have this information through the first generation (F_1) after a release, since most of the radiation-induced deleterious effects are manifested at this time.

Many environmental perils await larvae that are reared on whorl-stage corn compared to larvae reared in the safety of a laboratory insectary. For example, corn infested in the late whorl-stage provides some protection for the larvae through the third instar; however, once the tassel emerges, the larvae must relocate to the ear or another whorl-stage plant to maintain a food source and some degree of protection. Other perils encountered by the larvae include wider temperature extremes, rainfall, and exposure to parasitoids, predators, and pathogens. Larvae from irradiated parents were expected to exhibit even more deleterious effects when reared under field conditions than under laboratory conditions, since the environment in the field was less favorable. However, the data from this study indicate that the survival of F_1 NxN larvae is reduced more by the field rearing conditions than survival of larvae from irradiated parents, especially TxN and TxT larvae (Table 10). Apparently, the radiation-induced deleterious effects that reduce the survival rate of larvae from irradiated parents under

laboratory conditions are partially obscured by the natural mortality factors present under field conditions. This situation enhances the probability that an F_1 mating would involve progeny from irradiated parents and therefore favors the use of inherited sterility as a control method.

Effects of Radiation and Inherited Sterility on Mating Competitiveness

The greatest single disadvantage in the use of radiation-sterilized male moths to control lepidopteran populations has been considered the failure of irradiated males to compete successfully with normal males (North and Holt 1970). Data from field-cage studies reported in Chapter Five suggest that laboratory-reared male and female CEW irradiated with 10 krad are competitive with normal laboratory-reared moths in mating, and that this competitiveness is not altered by the time interval between irradiation and release or by the mating status of the male and the time interval between mating and release. Male progeny from irradiated (10 krad) males x normal females are competitive with normal males in searching for and securing mates (Table 12).

The field studies reported in Chapter Five were conducted during moderately high wild population densities. During the studies in the tobacco fields, wild virgin females frequently fed from tobacco blooms but left the fields before mating. Wild males fed from the tobacco blooms but remained in the field long enough to mate with laboratory females or to be captured in the traps. A different situation occurred during the studies in cotton. Host plants near or adjacent to the cotton field were senescent, and in certain areas, attractive plants had been

destroyed. Therefore, many CEW adults with various mating histories were attracted to the cotton.

Competition for mates was reduced for early-calling females (laboratory and/or virgin) but increased for males under the field situations described above. In the tobacco fields, an abundance of males was present, whereas in the cotton field, many of the females had been mated and either tended to call at a later time than virgins or declined to mate. Thus, calling virgin females were mated readily in both situations.

Male competitiveness was measured by the number of males captured in traps and observed in copula. Male trap capture exhibited the ability of a male moth to detect the pheromone, initiate oriented flight, locate the pheromone source, and enter the trap. Except for the ability to execute these activities, no competition between males was evident, since the traps accepted many males simultaneously. The incidence of males in copula demonstrated a greater amount of male competitiveness. Not only was it necessary for males to detect and find the pheromone source (calling females), but the males also had to compete directly with each other once they approached a calling female. Often 10 or more males, grouped in a pack, responded to the same calling female. Sparks et al. (1979) reported that H. virescens males also respond as a group to individual calling females, and they discussed the factors that precipitate this behavior.

Calling CEW females were often approached (< 5 cm) 10-20 times by males within a pack before copulation was achieved. The factors responsible for mate selection under these conditions are unknown. Nevertheless, the data from these studies indicated that irradiated (10 krad)

males were competitive with normal males and that laboratory-reared males were competitive with wild males under the conditions imposed upon them by these studies.

Mating Propensity of Females With Different Mating Histories

Irradiated male Lepidoptera may be competitive in mating but produce sperm that is not fully effective (Proverbs and Newton 1962, Flint and Kressen 1968). In Heliothis, sperm within a female from a previous mating is partially or completely displaced by the sperm of a later mating (Flint and Kressen 1968, Pair et al. 1977). Therefore, it is important for a mating with a genetically altered male to elicit the same ovipositional and mating behaviors from females as a mating with a normal male. If the sperm from a genetically altered male reduces the fecundity and intermating interval (length of time between female copulations) of a female, the sperm from a normal male would be more competitive.

CEW females containing irradiated (17.5 and 35 krad) sperm are as attractive as virgin females, while females containing normal sperm are significantly less attractive (Snow et al. 1972). However, the data reported in Tables 19 and 21 indicate that females mated to normal males and males irradiated with 10 krad have the same mating propensity and experience the same intermating interval. The sperm competitiveness demonstrated by these irradiated males is reduced in F_1 males. Females mated to male progeny from irradiated (10 krad) males outcrossed to normal females exhibited the same attractiveness and mating propensity as virgin females (Tables 20 and 22).

CHAPTER EIGHT
GENERAL CONCLUSIONS

The effects of substerilizing doses of radiation and inherited sterility on the reproductive ability and behavior of the CEW suggest that a great potential exists for population suppression. This research found the following: (a) a 10-krad dose of radiation can induce deleterious effects which are inherited through the F_2 generation, (b) radiation-induced deleterious effects are similar to those of other species of Lepidoptera, (c) the relationship between the survival of normal larvae and larvae from irradiated (10 krad) parents was similar under laboratory and field rearing conditions, (d) male and female CEW irradiated with 10 krad are competitive with normal moths in mating, and this competitiveness is not altered by the time interval between irradiation and release or by the mating status of the male and the time interval between mating and release, and (e) females mated to normal males and males irradiated with 10 krad have the same mating propensity and experience the same intermating interval. These results are encouraging; however, continued studies on reproduction, mating competitiveness, dispersal, rearing technologies, and population dynamics are required to further define the usefulness of radiation and inherited sterility as components of an area-wide management system for the CEW. Priority research objectives include the following: (a) study the interactions of inherited sterility and CEW diapause, (b) compare the development of larvae from normal and irradiated parents on substandard diets and

resistant varieties of corn, (c) compare the resistance/susceptibility of larvae from normal and irradiated parents to different insecticides, (d) continue investigations on the mating and sperm competitiveness of irradiated CEW and their progeny, (e) improve technologies for rearing, irradiating, and releasing CEW, and (f) further define the role of migration and dispersal in the population dynamics of the CEW. A full evaluation of this control strategy also necessitates the development of population models that will evaluate all available data and identify areas of needed research. Additionally, an economic assessment (which considers both cost of project and environmental savings) is required to aid in deciding if and when such a control strategy should be implemented.

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BIOGRAPHICAL SKETCH

James Edgar Carpenter, son of Mr. and Mrs. James Albert Carpenter, Jr., was born June 6, 1955, in Dothan, Alabama. He attended elementary and junior high school in Echo, Alabama, and graduated from Dale County High School in 1973. Upon receiving a B.S. degree from Troy State University in 1976, he accepted an agricultural research technician position at the USDA-ARS Southern Grain Insects Research Laboratory in Tifton, Georgia. He returned to school in 1979 and completed the requirements for his M.S. in entomology from the University of Georgia in 1980. He then continued his work at the Southern Grain Insects Research Laboratory as a research entomologist, a position he currently holds. He began studying for his Ph.D. in entomology at the University of Florida in 1983.

Mr. Carpenter is a member of the Entomological Society of America, the Georgia Entomological Society, the American Registry of Professional Entomologists (associate), and Sigma Xi.

He married Brenda Kay Mathews in 1974. They have two children, James Matthew and Anna Marie.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Harvey L. Cromroy, Chairman
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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